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Lystrosaurus from Antarctica

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ABSTRACT

The Lower Triassic therapsid reptile *Lystrosaurus*, first discovered in Antarctica in 1969, is now known from rather abundant materials collected from the Fremouw Formation at Coalsack Bluff, Graphite Peak, and McGregor and Shackleton glaciers, during the two field seasons of 1969–1970 and 1970–1971. Two species, *L. murrayi* and *L. curvatus*, are identified from portions of skulls, both species having been originally described from South African specimens. The bulk of the Antarctic fossils, consisting of postcranial elements is not specifically identified, but is described and figured. Included are tusks, a stapes, vertebrae, the shoulder girdle and forelimb elements, and the pelvic girdle and hind limb elements. The 31 described species of *Lystrosaurus* are reviewed, and it is suggested that these probably should be reduced to eight or nine, contained within two evolutionary lines, as proposed by Cluver (1971). These are on the one hand *Lystrosaurus curvatus* (the most primitive species), *L. platiceps*, and *L. rajurkari*, and on the other *L. murrayi*, *L. mccaigi*, *L. declivis*, and *L. hedini*. *Lystrosaurus oviceps* may be included with the first of the above-named groups, or it may be an intermediate form. *Lystrosaurus weidenreichi*, known largely from the postcranial skeleton, is of indeterminate status. The species central to the two lines, *L. curvatus* and *L. murrayi*, may represent a primary radiation of the genus through an ancient Gondwanaland. The presence of these two species in Antarctica provides very strong evidence for the connection of Antarctica with Africa. *Lystrosaurus murrayi* in India bolsters the evidence that the Indian peninsula likewise was a part of Gondwanaland. *Lystrosaurus murrayi* (as well as other species) in China may lend weight to the proposal, advanced by

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Hurley (1971) and others, that China might have been a portion of the Gondwanaland continent. Alternatively the Chinese forms may have reached eastern Asia by a long migration.

INTRODUCTION

The reptilian genus *Lystrosaurus*, so characteristic of those Lower Triassic sediments known as the Middle Beaufort Beds, or alternatively as the *Lystrosaurus* Zone in the Karroo sequence in South Africa, was first definitely recognized in Antarctica on December 4, 1969. On that day a right maxilla with a tusk was discovered in the Lower Triassic Fremouw Formation at Coalsack Bluff in the Transantarctic Mountains, at approximately latitude $84^{\circ} 15' S$, longitude $162^{\circ} W$ —a locality about 400 miles or 600 km. from the South Pole. The specimen was found by James A. Jensen of Brigham Young University, a member of a field party working at Coalsack Bluff.¹

Numerous other specimens of *Lystrosaurus* were found in Antarctica during the course of the two field seasons. Those at Coalsack Bluff consisted of isolated bones that had been transported and deposited in stream-channel sediments. Those at McGregor Glacier consisted not only of single bones, but also of associated and partially articulated materials. This latter locality was up the paleoslope from the Coalsack Bluff site, so that specimens were commonly in fine and often indurated sediments, and thus had not been scattered as a result of stream action. It should be added that some additional material was found on the slope of Graphite Peak during the second season of collecting, at about latitude $85^{\circ} S$, longitude $172^{\circ} W$, more or less midway between Coalsack Bluff and McGregor Glacier. It was at the Graphite Peak locality that the first Triassic tetrapod

¹ Two paleontological field parties worked in the Transantarctic Mountains during two successive seasons, for the express purpose of discovering and excavating Lower Triassic tetrapods. The party of the first season, the austral summer of 1969–1970, working at Coalsack Bluff, consisted of Edwin H. Colbert as the leader; William J. Breed of the Museum of Northern Arizona, Flagstaff; James A. Jensen of Brigham Young University, Provo, Utah; and Jon S. Powell of the University of Arizona, Tucson. The party of the second season, the austral summer of 1970–1971, working at McGregor Glacier, at approximately latitude $85^{\circ} 15' S$, longitude $176^{\circ} E$, consisted of James W. Kitching of the Bernard Price Institute of Paleontology, University of the Witwatersrand, Johannesburg, Union of South Africa, as leader; John Ruben of the University of California, Berkeley; and, for a short time, Thomas Rich of Columbia University, New York. Both parties, which were sections of larger geological study units, were under the overall leadership of David H. Elliot of the Institute of Polar Studies of the Ohio State University, Columbus. All the work was done under the auspices of the National Science Foundation of the United States of America.

was discovered in Antarctica—a fragment of a labyrinthodont amphibian lower jaw, found by Peter J. Barrett in December, 1967.

At least 150 recognizable fossils of *Lystrosaurus* have been collected in Antarctica up to the present time. Many of these are, of course, fragmentary and therefore not particularly useful except as records indicating the relative abundance of the genus in the Fremouw Formation. At least 30 or 40 specimens are, however, significant for the purposes of diagnostic and comparative studies, and some of these are described and illustrated in the present paper. In short, *Lystrosaurus* in Antarctica is now sufficiently well known from good materials so that studies of its relationships can be carried on with confidence.

It is the purpose of the present paper to identify the *Lystrosaurus* fossils from Antarctica, and to demonstrate their relationships with *Lystrosaurus* found in other parts of the world, especially as it is known from South Africa.

The fossils described herein were prepared by Mr. David Lawler and Miss Camas Lott. The drawings were made by Miss Pamela Lungé, the photographs by Mr. Marc Gaede. The work was supported in part by a grant from the National Science Foundation, no. GV-25341.

MATERIALS AND LOCALITIES

From the Fremouw Formation, Lower Triassic, Transantarctic Mountains, the following specimens of *Lystrosaurus* were collected from sandstone cliffs of the second sandstone-siltstone cycle of the three-cycle sequence, exposed along the northwest slope of Coalsack Bluff.

- AMNH¹ 9302, right maxilla of a small individual, with tooth
- AMNH 9303, left ulna
- AMNH 9304, distal portion of a left humerus
- AMNH 9306, centrum of a thoracic vertebra
- AMNH 9307, centrum of a thoracic vertebra
- AMNH 9308, left maxilla, lacking tooth
- AMNH 9311, portion of left quadrate
- AMNH 9317, left tibia
- AMNH 9318, right ilium, incomplete
- AMNH 9320, right ischium
- AMNH 9322, left femur
- AMNH 9324, phalanx
- AMNH 9325, phalanx
- AMNH 9327, centrum of a thoracic vertebra
- AMNH 9328, centrum of a thoracic vertebra

¹ The American Museum of Natural History, New York.

- AMNH 9349, left pubis
- AMNH 9350, right femur, lacking ends
- AMNH 9351, proximal portion of right femur
- AMNH 9352, distal portion of right femur
- AMNH 9353, distal end of right fibula
- AMNH 9356, left stapes
- AMNH 9359, distal end of fibula
- AMNH 9360, portion of left ischium
- AMNH 9364, two tusks, not associated
- AMNH 9365, 19 vertebral centra, not associated, and some incomplete
- AMNH 9366, sacral vertebra
- AMNH 9369, distal ends of two humeri, not associated
- AMNH 9371, proximal ends of two femora, not associated
- AMNH 9374, proximal end of metapodial and a phalanx, not associated
- AMNH 9376, portion of a right ischium
- AMNH 9377, portions of two ischia, not associated
- AMNH 9378, acetabular region of a small ilium
- AMNH 9379, portions of left fibula

The following specimens were collected from the north end of Coalsack Bluff, in sandstones correlative with the second sandstone cliff of the main exposures.

- AMNH 9314, distal portion of right humerus
- AMNH 9321, left femur
- AMNH 9372, distal end of femur (from north end of Coalsack Bluff)
- AMNH 9373, distal end of radius (from high saddle at north end of Coalsack Bluff)

The following specimens were collected from sandstones correlative with those of the "upper" exposures at Coalsack Bluff, but in what may be either the lower limb of a monoclinal fold or a downthrown fault block near the base of the northwest slope of the Bluff. The sediments are essentially vertical. The specimens are from a small quarry developed in the upturned second sandstone and from contiguous sites along the strike.

- AMNH 9305, block of matrix, containing several bones and a large, faceted tooth
- AMNH 9310, tooth
- AMNH 9312, portion of right articular
- AMNH 9313, proximal portion of left humerus
- AMNH 9315, portion of left scapula
- AMNH 9316, left ulna
- AMNH 9319, right ischium
- AMNH 9326, centrum of a thoracic vertebra
- AMNH 9329, tooth
- AMNH 9354, right radius
- AMNH 9355, distal end of left humerus, weathered
- AMNH 9357, portion of right maxillary antrum and lacrimal
- AMNH 9358, portion of left humerus

- AMNH 9361, a tusk, and a tusk fragment, associated
- AMNH 9362, three tusks, not associated
- AMNH 9363, tusk showing wear facet
- AMNH 9367, three vertebral centra, not associated
- AMNH 9370, proximal end of right ulna
- AMNH 9375, several phalanges and a metatarsal
- AMNH 9380, portions of two tibiae, not associated
- AMNH 9381, distal end of a left radius

The following specimen is from an erratic block at Cherry Icefall, approximately 40 miles or about 60 km. east by south of Coalsack Bluff.

AMNH 9368, vertebral centrum, found by Donald Coates

In addition, there are numerous specimens from Coalsack Bluff, too fragmentary or of too indeterminate a nature to be numbered.

The following specimens were collected in the Shackleton-McGregor glacier area during the 1970-1971 field season. The locality for each specimen is listed separately.

- AMNH 9505, large "snout," crushed; *Thrinaxodon* Col.
- AMNH 9514, right scapula, distal part of humerus, radius, part of manus, rib of a large individual, associated; *Thrinaxodon* Col.
- AMNH 9515, left side of a skull, with a sagittal section exposed in the rock; Half-moon Bluff, Sentinel Hill
- AMNH 9530, left scapula, humerus, ulna, fragments of two long bones, associated, small individual; *Thrinaxodon* Col.
- AMNH 9565, "rib cage" and two digits of a foot; Kitching Ridge
- AMNH 9566, a conglomeration of crushed bones in rock, probably representing one or more skeletons; Halfmoon Bluff, Sentinel Hill

The following specimens were collected at Graphite Peak, about midway between Coalsack Bluff and Shackleton-McGregor glaciers, and near the site where the first Antarctic Triassic tetrapod (a portion of a labyrinthodont jaw) was discovered.

- AMNH 9559, portions of a small individual, including the left scapula and fragment of right scapula, sternum, coracoids and precoracoids, clavicles, right humerus, radius and ulna, left humerus, radius and ulna (in articulation), metapodials and phalanges, several vertebrae and ribs
- AMNH 9567, a fragmentary skull in a friable matrix

STRATIGRAPHIC RELATIONSHIPS

The name "Beacon Sandstone Formation" was proposed in 1907 by H. T. Ferrar, a member of the *Discovery* expedition, to designate the essentially horizontal continental deposits as typically exposed at Beacon

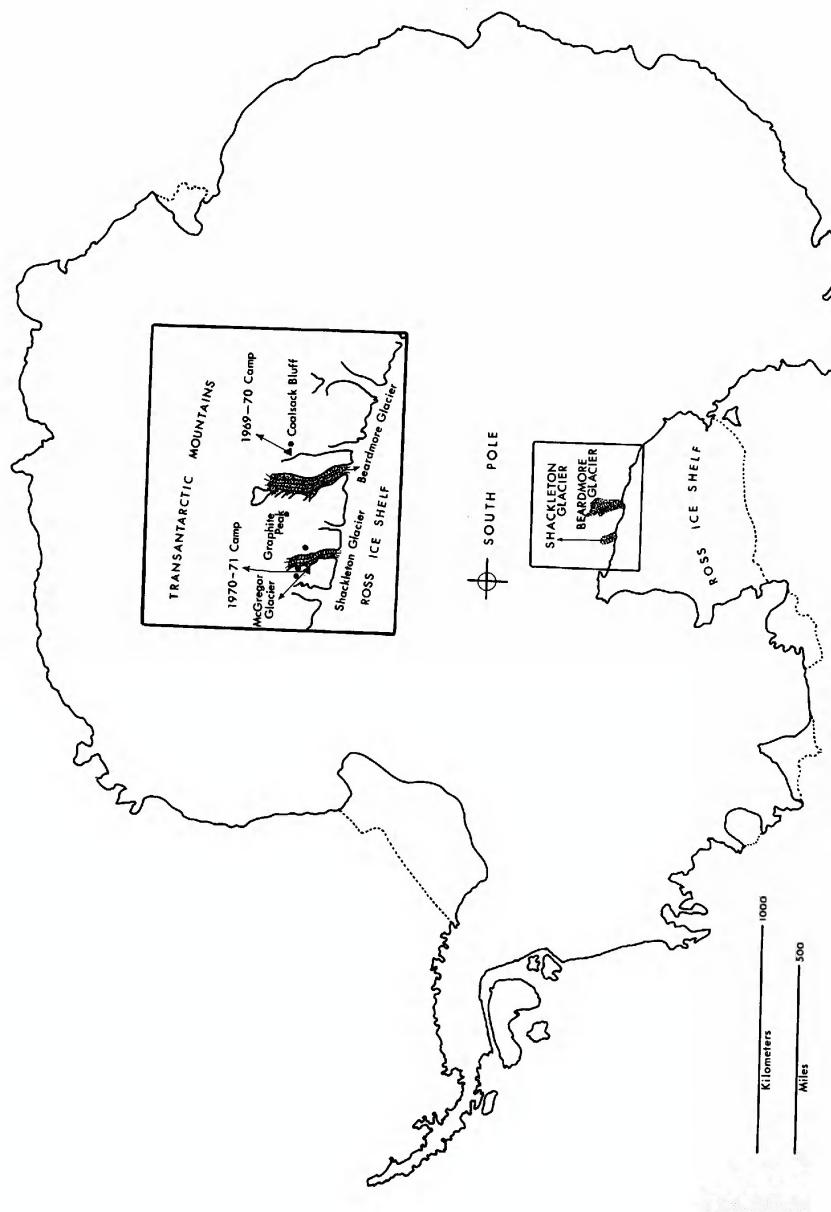


FIG. 1. Outline map of Antarctica showing location of Beardmore and Shackleton glaciers in relation to South Pole and Ross Ice Shelf. Camps (triangles) and collecting localities (circles) are shown in inset.

Heights at the upper end of the Taylor Glacier, this locality being in the mountains across the Ross Ice Shelf from, and about 85 miles due west of, Hut Point on Ross Island, where Scott had established his base. In the course of time it became apparent that the Beacon sediments did not constitute a single geological unit, but rather a series of formations covering a considerable span of geologic time. Moreover, it became evident that Beacon rocks are widely distributed in the Transantarctic Mountains, the magnificent range or series of ranges that cross Antarctica from Victoria Land to the Weddell Sea.

The first clue as to the age of some of the Beacon rocks came in 1912, when Scott and his little party, on their fatal return trip from the South Pole down the immense Beardmore Glacier, observed Beacon rocks and collected samples that included fossils of the Permian plant, *Glossopteris*. These specimens were found with the bodies of Robert Falcon Scott, Edward Wilson, and Henry Robertson Bowers at their last camp, about 11 miles from One Ton Depot on the Ross Ice Shelf.

Of course these fossils pointed to a close relationship between those Beacon sediments in Antarctica bearing *Glossopteris*, and *Glossopteris* sediments in other continental regions, namely South Africa, peninsular India, Australia, and South America.

In 1958 H. J. Harrington suggested that the term Beacon System be applied to the late Paleozoic and early Mesozoic continental sediments widely exposed in the Transantarctic Mountains, and he further suggested that the term Beacon Group be used for the rocks in the type area. Since that time the use of the term Beacon Group has become well established for late Paleozoic and early Mesozoic continental rocks as they are exposed through a considerable portion of the Transantarctic Mountains.

The Beacon Group in the region of the Beardmore Glacier was divided into six formations by G. W. Grindly in 1963. Subsequently two more formational units were recognized by P. J. Barrett in 1969 and by J. F. Lindsay in that same year. Consequently the Beacon Group is now considered as being made up of eight formations, ranging in age from possibly the Devonian to the Jurassic. Table 1 suggests the sequence.

As is evident from table 1, the Fremouw Formation is not only the lowest but also the thickest of the Triassic units within the Beacon Group. It is separated from the underlying Permian Buckley Formation by a disconformity that probably represents a considerable time hiatus. The Buckley Formation is a sequence of mudstones, black, carbonaceous shales, and coal beds, with at places remarkably abundant deposits of *Glossopteris* leaves in the black shales. This is especially true at Coalsack Bluff, where not only is there a wealth of *Glossopteris* in the middle and

TABLE 1

CORRELATION OF BEARDMORE GLACIER AND SHACKLETON GLACIER FORMATIONS AS THEY RELATE TO BEACON GROUP

Age	Group	Beardmore Glacier Formations	Shackleton Glacier Formations	Description
		Kirkpatrick Basalt 600+ m.		Tholeiitic flows, interbeds with holostean fish and conchos- tracans
Jurassic	Ferrar	Ferrar Dolerite 1000 m. (Intruded into Beacon sediments)		Sills and a few dikes
Disconformity				
		Prebble 3-460+ m.		Mudflow, pyro- clastic breccia, tuff, tuffaceous sandstone
		Falla 160-530 m.	Falla 200+ m.	Volcanic sand- stone, shale; tuff in upper portion <i>Dicroidium</i>
Triassic	Beacon	Fremouw 650 m.	Fremouw 700+ m.	Subarkose and arkosic volcanic sandstone, shale, greenish gray mudstone
				Logs, coal, <i>Dicroidium</i> near top
				<i>Lystrosaurus</i> , <i>Thrin-</i> <i>axodon</i> and other therapsids; <i>Procolophon</i> ; eosuchians; labyrinthodont amphibians near base
Disconformity Disconformity				

TABLE 1—(Continued)

Age	Group	Beardmore Glacier Formations	Shackleton Glacier Formations	Description
Permian	Beacon	Buckley 750 m.	Buckley 450 m.	Arkosic and volcanic sandstone, dark gray shale, coal <i>Glossopteris</i>
		Fairchild 130–220 m.	Fairchild 200 m.	Massive subarkosic and arkosic sandstone
		Mackellar 60–140 m.	Mackellar 160 m.	Dark shale, fine-grained sandstone
		Pagoda 125–395 m.	Pagoda 4–190 m.	Tillite, sandstone, shale
Disconformity		Unconformity		
Devonian?		Alexandra 0–330 m.		Quartz arenite, sandstone

upper portions of the Formation, but also numerous coal beds. Logs are present, too, and the development of strong annular rings in these fossil logs indicate a climate marked by an alternation of seasons. It seems evident that the Buckley Formation was deposited on a floodplain under conditions that favored the abundant growth of plants.

There is an abrupt change of lithology between the top of the Buckley Formation and the base of the Fremouw Formation which, among other criteria, gives evidence of a time gap between the two units. Another interesting point is that there is a complete reversal of paleocurrent directions from the one formation to the other. In the Permian the ancient current directions were toward the southeast; in the Triassic, as is nicely indicated by Fremouw lithology, current directions were toward the northwest.

The Fremouw Formation, like the Buckley, also was deposited on a freshwater floodplain, but instead of the dark shales and coals that characterize the Permian beds, the Fremouw consists of cyclic brownish, gray,

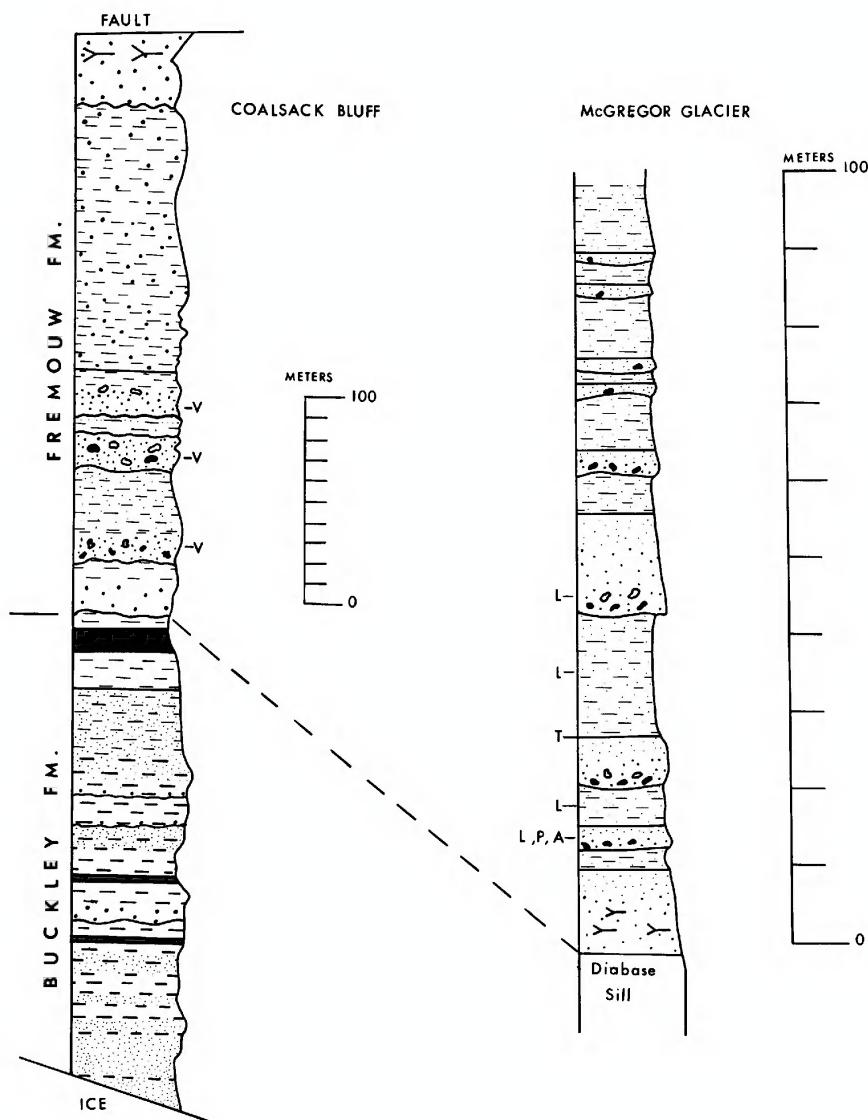


FIG. 2. Sections of vertebrate-bearing beds at Coalsack Bluff and at McGregor Glacier, Antarctica.

Symbols: A, amphibians; L, *Lystrosaurus*; P, *Procolophon*; T, *Thrinaxodon*; V, vertebrates.

and reddish sandstones, siltstones, and mudstones. The fossil bones are found in the lower part of the formation; the upper portion contains fossil logs and fronds of the Triassic Southern Hemisphere plant, *Dicroidium*. It may be helpful to describe the Fremouw Formation from Kitching et al. (1972, pp. 524-525):

"All fossil-bone localities in the Shackleton Glacier area are in the lower 200 m of the 700 m+ thick Fremouw Formation. At Coalsack Bluff bones were found as far as 120 m above the base of the formation in similar rocks. From the Queen Alexandra Range to the Queen Maud Mountains the lower part of the Fremouw Formation is a cyclic unit consisting of one to several fining-upward cycles typical of fluvial deposition. A cycle begins at the base with a coarse channel sandstone that contains intraformational conglomerate. At some localities these intraformational conglomerates contain disarticulated bones. Most clasts are the same mudstone as the beds beneath the erosion surface into which the channel is cut. They are presumed to have been derived from older fine-grained floodplain deposits. Each cycle grades upward to medium and fine sandstone, then to green-gray mudstone in which skeletal material is found. This part of the Fremouw Formation is readily recognized by thick resistant sandstone ledges, which contrast with the non-resistant dominantly mudstone of the middle part of the Fremouw Formation, and with the slope-forming carbonaceous beds of the underlying Permian Buckley Formation."

Shackleton Glacier where the collections of the second season were made is about 150 miles or approximately 250 km. up the paleoslope from Coalsack Bluff, where the collections of the first season were made, and therefore nearer the sources of the floodplain deposits. It is a site of articulated skeletons contained within fine-grained sediments, as contrasted with the disarticulated bones contained within rather coarse-grained channel deposits so typical of the Coalsack Bluff locality. Thus there are differences in the preservation of the fossils between the two localities, quite apparent when the collections from the two regions are compared. Because of these differences in deposition, the two collections augment each other in a most interesting fashion. The isolated bones from Coalsack Bluff lack the advantage of association with other skeletal elements, but they have the virtue of being rather easily removed from the sandstones in which they were deposited, thus affording good specimens that can be studied "in the round." The materials from Shackleton Glacier, in contrast, have the decided advantage of containing numerous articulated skeletons or partial skeletons. The disadvantages of these materials are the frequently indurated sediments in which they are contained, more often

than not making the complete removal of bones from the rock virtually impossible. Moreover, many of the specimens from Shackleton Glacier are in the form of natural molds in the rock from which the bone has weathered away. Thus it is necessary to study the materials from casts made from these molds. In spite of these contrasts, advantages, and disadvantages, the fossils from Coalsack Bluff and Shackleton Glacier, taken together, afford a truly comprehensive view of the Lower Triassic Fremouw fauna, one of inestimable value for comparison with faunas of similar age in other continental regions. There is every reason to think that future work in Antarctica will add greatly to the Fremouw fauna, not only as additional better materials of forms already identified are found, but also as new elements are added.

Above the Fremouw Formation is the Falla Formation, which so far has yielded *Dicroidium*. This unit contains volcanic rocks, of which Strontium-Rubidium analyses give an age of 203 ± 12 million years. Such an age confirms the evidence of the fossils in the underlying Fremouw Formation as to the Lower Triassic affinities of this latter unit.

The Falla Formation constitutes the top of the Beacon sequence in the Shackleton Glacier area; in the Beardmore region the Falla Formation is topped by the Prebble Formation, still another Triassic unit, and it in turn is separated from the overlying Jurassic volcanics by a disconformity.



FIG. 3. *Lystrosaurus murrayi* (Huxley), AMNH 9302, right maxilla with tusk, lateral view. $\times 1$.

DESCRIPTIONS OF FOSSILS

SYSTEMATICS

CLASS REPTILIA

ORDER THERAPSIDA

SUBORDER ANOMODONTIA

INFRAORDER DICYNODONTIA

FAMILY LYSTROSAURIDAE

LYSTROSAURUS COPE, 1870*Lystrosaurus murrayi* (Huxley)

ANTARCTIC SPECIMENS UNDER CONSIDERATION: AMNH 9302 and 9308, a right and a left maxilla, respectively.

As mentioned, the first undoubted specimen of *Lystrosaurus* found in Antarctica was the fossil discovered on December 4, 1969. AMNH 9302 is a right maxilla with a tusk, representing a small individual. It has been cited and figured in previous papers, but no detailed comparisons have until now been published.

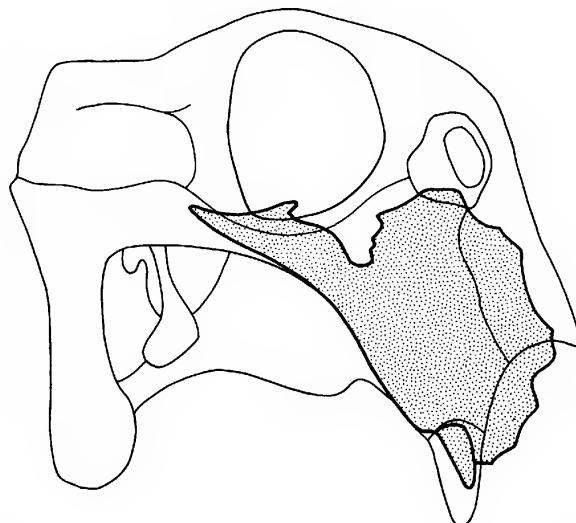


FIG. 4. Outline of skull fragment of *Lystrosaurus murrayi* from Antarctica (AMNH 9302), superimposed on outline of skull of *Lystrosaurus murrayi* from South Africa. Skull outline from Cluver, 1971. Skull fragment from Antarctica. $\times 1$.

There was no doubt as to the generic identity of this specimen, even in the field. It is definitely a dicynodont, and among the dicynodonts only *Lystrosaurus* has the elongated and downturned maxilla that is so conspicuous, even in this fragmentary specimen. This is nicely shown in figure 4, which represents an outline of the Antarctic specimen superimposed on an outline of the skull of *Lystrosaurus murrayi* taken from the recent monograph by Cluver (1971) on the cranial morphology of *Lystrosaurus*. The correspondence of the maxillary borders in the two specimens needs no emphasis here beyond what is shown in the figure. The resemblance of this Antarctic specimen to *Lystrosaurus* from Africa, specifically *Lystrosaurus murrayi*, is further illustrated by the close correspondence of the Antarctic fossil to a specimen (BPI¹ 413) in Johannesburg. The African specimen, which has been identified as *Lystrosaurus murrayi*, is a very young individual, more or less comparable in its ontogenetic development with the Antarctic specimen, although there is a difference between the two in the size of the tusks.

The Antarctic specimen, AMNH 9302, consists not only of a large part of the right maxilla with the included tusk, but also of a portion of the premaxilla, and of the septomaxilla, as indicated by the depression occupied by this bone in *Lystrosaurus*, which partially surrounds the nasal opening. The specimen also shows the shallow longitudinal depression in the maxilla, so characteristic of *Lystrosaurus*, between the region of the tusk and the nasal depression.

This specimen is nicely supplemented by another fossil from Coalsack Bluff, AMNH 9308, an uncrushed maxilla that shows to good effect the broad, almost flat bone surface formed by the ventral portion of the alveolus for the tusk. Posteriorly this ventral surface comes to a point, as a part of its articulation with the forward extension of the pterygoid bone. Anteriorly may be seen portions of the articular surfaces for the premaxilla and septomaxilla bones. Although AMNH 9308 represents an individual perhaps one-fourth larger than AMNH 9302, the disparity between the alveoli in the two specimens, and presumably of the tusks, is striking; the alveolus of AMNH 9308 is approximately twice the diameter of that in AMNH 9302. Perhaps this represents individual variation or some degree of sexual dimorphism. The alveolus in AMNH 9308 is of such a size as to have accommodated a tusk like that seen in a similar South African specimen of *Lystrosaurus murrayi*, BPI 106. The Antarctic specimen is illustrated in figure 6.

¹ Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg.

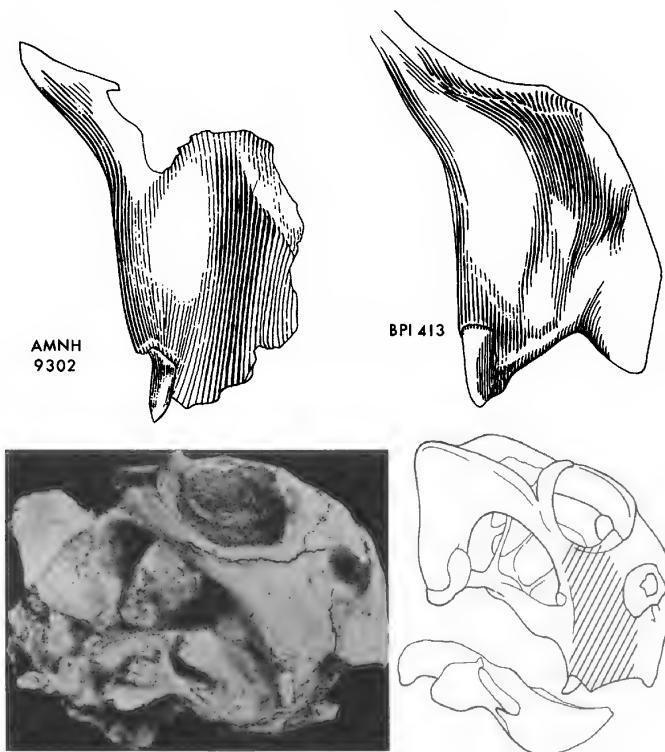


FIG. 5. *Lystrosaurus murrayi* (Huxley). AMNH 9302, $\times 1$; compared with same portion of a skull, BPI 413, from South Africa, $\times 1$. Complete skull and mandible, BPI 413, $\times 1/2$. Outline of skull and jaw of *Lystrosaurus murrayi*, showing position of fragments as above.

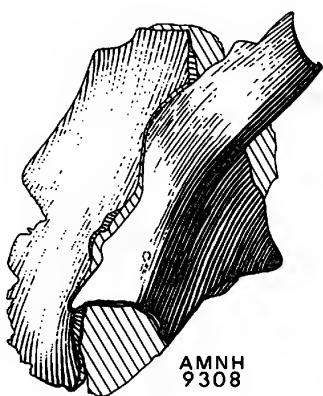


FIG. 6. *Lystrosaurus murrayi* (Huxley), AMNH 9308, portion of left maxilla with alveolus for tusk, lateral view. $\times 1$.



FIG. 7. *Lystrosaurus curvatus* (Owen), AMNH 9515, a natural longitudinal section through a skull. X1.

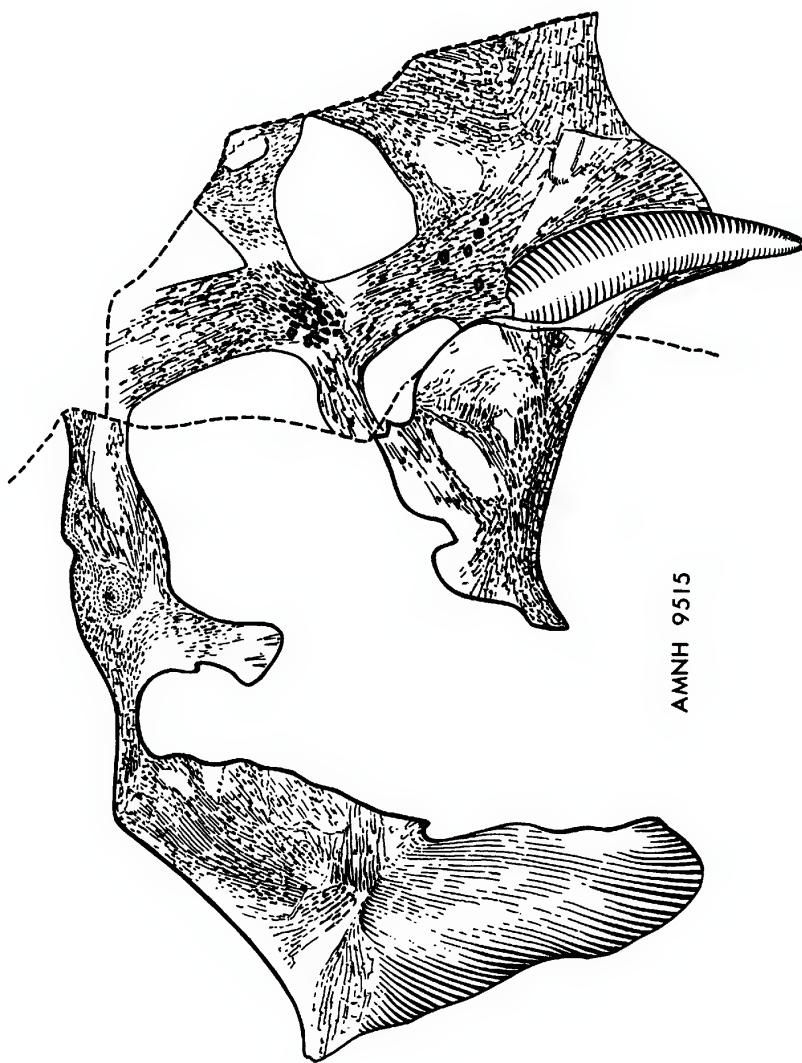


FIG. 8. *Lystrosaurus curvatus* (Owen), AMNH 9515, interpretation of specimen shown in figure 7. $\times 1$.

Lystrosaurus curvatus (Owen)

ANTARCTIC SPECIMEN UNDER CONSIDERATION: AMNH 9515.

A partial skull of *Lystrosaurus*, discovered by the expedition of 1970-1971, is particularly valuable because it provides some information about the shape of the skull in an Antarctic *Lystrosaurus*, when viewed laterally. The specimen consists of bone in the rock, showing a more or less medial section of the skull. Although incomplete, the specimen nevertheless is useful because it affords a satisfactory outline of the skull (except for the very front of the snout) and the position of the orbit and of the temporal fenestra (figs. 7, 8). A restoration of the outline of the skull is seen in figure 9, superimposed on the outline of *Lystrosaurus curvatus* from the *Lystrosaurus* Zone of South Africa figured by Cluver (1971). As can be seen, there is a close correspondence between the two. Therefore it is hereby suggested that this particular specimen, AMNH 9515, may reasonably be identified as *Lystrosaurus curvatus*. As in the African species, the Antarctic specimen is characterized by its relatively primitive shape for, as will be seen below,

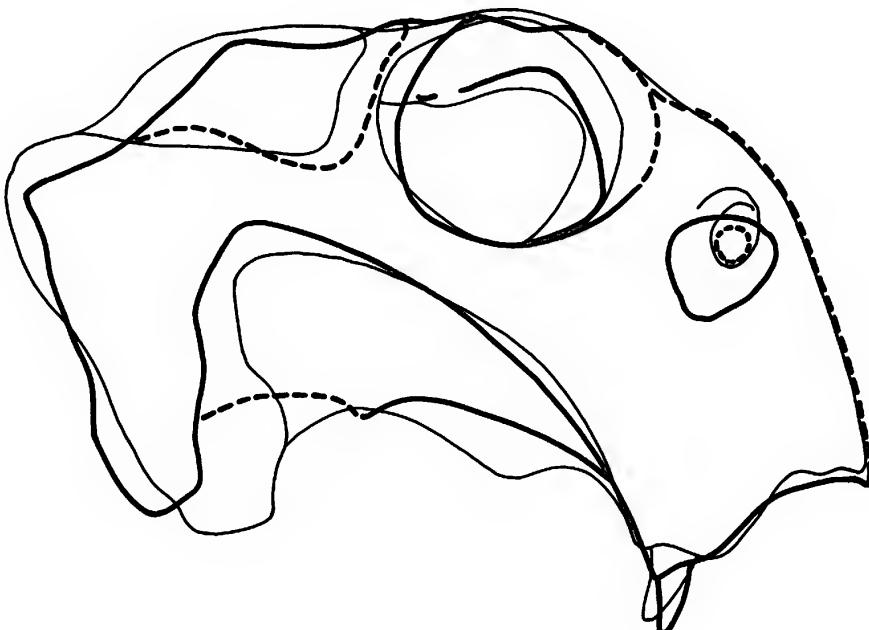


FIG. 9. *Lystrosaurus curvatus* (Owen). Outline (heavy lines) of skull from Antarctica (AMNH 9515), superimposed on outline (light lines) of skull from South Africa, after Cluver, 1971.

Lystrosaurus curvatus may be considered the most generalized of the African species of the genus, showing strong resemblances to the prototype dicynodont, *Dicynodon*. In *Lystrosaurus curvatus*, and seemingly in the Antarctic specimen here being considered, the skull is comparatively low, with the facial portion rounded and relatively short, not flattened, elongated, and produced down so that it forms essentially a right angle to the skull table as in *Lystrosaurus murrayi*. The size of the orbit and the position of the nares in the Antarctic specimen are essentially similar to what is seen in *Lystrosaurus curvatus*.

Lystrosaurus sp.

ANTARCTIC SPECIMENS UNDER CONSIDERATION: All the specimens listed on pages 3-5, with the exception of AMNH 9302 and 9308, described as *Lystrosaurus murrayi*, and AMNH 9515, described as *Lystrosaurus curvatus*.

TUSKS

There are numerous isolated tusks in the collection, for which no specific identification can be attempted. These tusks are interesting, however, in view of the size ranges, and especially because of the wear facets exhibited on some of them.

As for size, AMNH 9505 from McGregor Glacier, a rather fragmentary "snout" in which, nevertheless, one alveolus with portions of the tusk still adhering to its surface is preserved, represents a large *Lystrosaurus*. The diameter of the tusk of this specimen is closely comparable to the diameter of the tusk in the type of *Lystrosaurus murrayi* in the British Museum (Natural History). The tusk of the British Museum type is larger than any other of the *Lystrosaurus* types except for that of *Lystrosaurus mccaigi* (which has been presumed by some students to be a large *Lystrosaurus murrayi*). Consequently it is not unreasonable to suppose that the large alveolus from the Antarctic represents a fully adult specimen of *Lystrosaurus murrayi*. The portion of tusk, AMNH 9305, preserved in a heavy conglomerate from the lower site at Coalsack Bluff, is almost as large as AMNH 9505, so it is clear that large *Lystrosaurus* specimens are to be found widely distributed in Antarctica. Tusk sizes range downward to very small specimens, such as AMNH 9302, already described.

AMNH 9305 displays a very large wear facet (fig. 10). As is evident, this facet is on the outer surface of the tooth, which indicates that in life *Lystrosaurus* must have employed the tusks extensively in some fashion to cause such external abrasion. The wearing of the tusk in this manner is almost certain to be correlated with the feeding habits, but how is a matter of speculation.

Watson (1948, p. 870) has suggested that in *Dicynodon* there were lateral movements of the lower jaw, as "shown by the existence of wear facets on the inner surface of the canines, which could only have been made by contact with the lateral surface of the lower horny beak." It is difficult to imagine that the lateral movements of the lower jaw in *Lystrosaurus* could have been very extensive; indeed, as Watson demonstrated, and has been confirmed in detail by Crompton and Hotton (1967), the dominant movement of the jaw in *Lystrosaurus*, as in other dicynodonts, was anteroposterior. Such movement probably would cause the development of inner wear surfaces on the tusks.

One tusk from Antarctica, AMNH 9310, shows two wear facets on opposite sides of the tooth (fig. 10); a large one on the outer surface, comparable with the large facet on AMNH 9305, and a smaller one on the inner surface. Moreover, the end of this tooth contains a prominent notch—the result of wear—which makes it appear that this *Lystrosaurus* must have cut or shredded plant fibers by a lateral movement of the head. Similar double facets are present on another tusk, AMNH 9363.

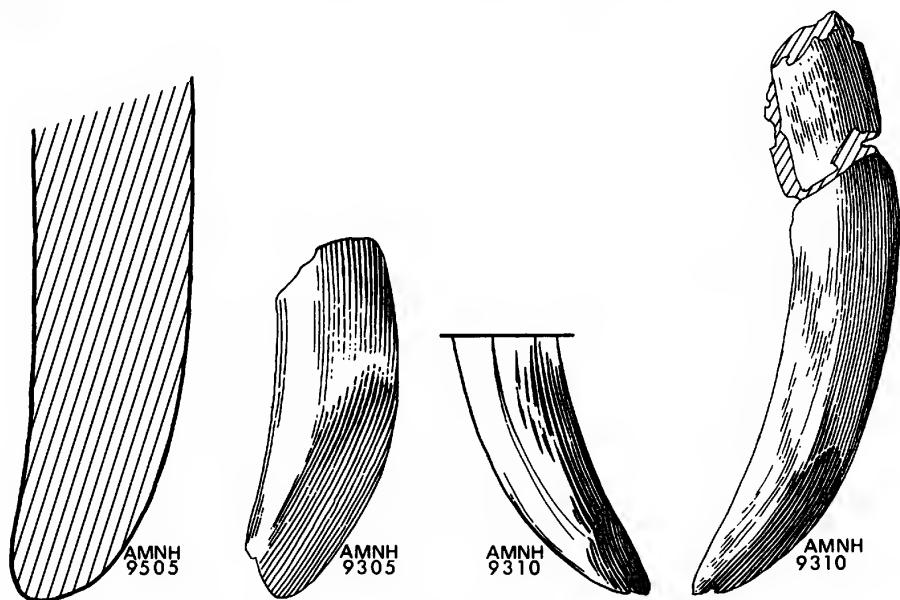


FIG. 10. *Lystrosaurus* sp., AMNH 9505, 9305, 9310. Tusks, AMNH 9505, drawn from an exposed alveolus showing maximum size of tusk presently known in Antarctic material. AMNH 9305 and 9310 showing wear facets on tusks, and in 9310 a notch at end of two wear facets (one on each side of tusk), presumably resulting from wear. All $\times 1$.

The presence of facets on the tusks, as seen in several specimens of *Lystrosaurus* from Antarctica, seems to add another dimension to the mechanics of alimentation in *Lystrosaurus*. Most reports on the jaw movements in this reptile stress the cutting function that necessarily played the dominant role in the trituration of the fibrous vegetation on which *Lystrosaurus* presumably fed. But the wear on the tusks indicates that these large teeth were important, too. Perhaps they were used for grubbing in the ground. The Antarctic tusk with the notch in the end is especially intriguing; it seems to indicate grubbing or digging, and, as mentioned, some side-to-side movement of the head, perhaps to break fibers or whole plants loose from their anchorages.

STAPES

An interesting specimen from Coalsack Bluff is an isolated left stapes, AMNH 9356. It is similar to various examples of *Lystrosaurus* stapes that have been described, as well as to a nicely preserved stapes of *Lystrosaurus murrayi* in the American Museum collection, available for comparative studies.

As is characteristic of the stapes in *Lystrosaurus*, the Antarctic specimen is short and broad, its anteroposterior width being not much less than the dimension along its long axis, that is, from the footplate to the lateral extremity. Dorsally the bone is strongly concave, ventrally it is flat. The footplate is a bosslike expansion, which would have fitted into a large *fenestra ovalis*. The lateral end of the bone, although somewhat incomplete, shows the dorsoventral flattening typical of the stapes in *Lystrosaurus*, and there is some evidence of the dorsal and ventral facets, described by Cluver (1971). As Cluver has shown, the dorsal facet articulates with the ventrolateral extremity of the opisthotic, whereas the ventral facet meets the ventromedial surface of the quadrate. Barry (1968) has described a median ventral facet on the stapes of *Lystrosaurus*, for the reception of the end of an ossified ceratohyal. Such a facet is not readily distinguishable

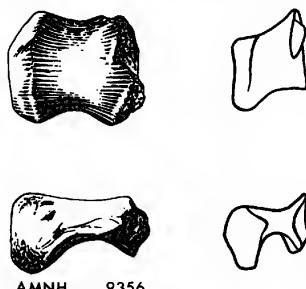


FIG. 11. *Lystrosaurus* sp., AMNH 9356, left stapes. Dorsal and posteroventral views, compared with same views of left stapes of *Lystrosaurus declivis* (after Cluver, 1971). Both $\times 1$.

on the Antarctic specimen, but it may very easily have been obliterated by weathering.

This bone is so very like the stapes in *Lystrosaurus murrayi* that it might be given this specific identification. In view of its lack of association with a skull, however, it is not as yet formally so designated.

POSTCRANIAL ELEMENTS

We now come to a consideration of the postcranial skeleton, represented by numerous isolated and some associated bones in the Antarctic collection. It is interesting, and perhaps amazing, to note that in spite of the thousands of specimens of *Lystrosaurus* that have been collected in Africa, there is a singular lack of published descriptions or illustrations of the postcranial skeleton in this important reptilian genus. Indeed, the preoccupation with skulls and the neglect of postcranial skeletons is an all too common fault of the literature on Karroo tetrapods. This may be the result of an embarrassment of riches. Students of Karroo tetrapods have been swamped by the volume of fossils available to them; therefore it is natural that time and effort for preparation and research have been concentrated on the skulls. To most students, up to the present, anything more than passing attention to the postcranial skeleton of *Lystrosaurus* has seemed like an unnecessary diversion. Certainly the delineation of trivial differences among the postcranial elements of *Lystrosaurus* admittedly poses a difficult, perhaps an insoluble, problem but it would be helpful if someone could look into this at some future date. Even though the prospect appears to be discouraging, a detailed study of postcranial bones definitely associated with identifiable skulls may yield interesting results. There are seemingly enough specimens in South African collections for such an attempt to be made.

Of course the lack of detailed information about the postcranial bones in African species of *Lystrosaurus* has made difficult the study of the Antarctic fossils, in which such bones predominate. Recourse necessarily has been had to two papers by Chung-Chien Young (1935, 1939) on *Lystrosaurus* from Sinkiang, in which entire skeletons are described and illustrated. These publications have been most helpful.

In the present paper various postcranial elements from Antarctica are briefly described, not only to show their resemblances to (or differences from) corresponding *Lystrosaurus* bones found in Africa and Asia, but also to give some idea of the nature and extent of *Lystrosaurus* fossils so far collected in Antarctica.

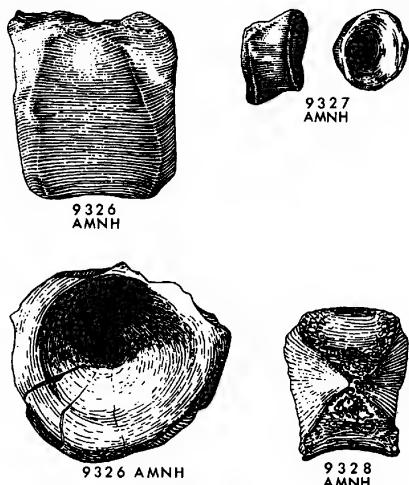


FIG. 12. *Lystrosaurus* sp., AMNH 9326, 9327, 9328, vertebrae. Anterior and lateral views of AMNH 9326 and 9327. AMNH 9328 shows longitudinal section in lateral view; close approximation of amphicoelous surfaces in middle of centrum is apparent. All $\times 1$.

VERTEBRAE

Among the first fossils found at Coalsack Bluff were vertebral centra of *Lystrosaurus*. Three of these are shown in figure 12. They are drawn to the same scale and illustrate the range in size seen among the vertebrae, AMNH 9326 being one of the largest and AMNH 9327 one of the smallest. The former is about 36 mm. in diameter and thus represents a large individual; the latter, about 13 mm. in diameter presumably came from a small animal, or perhaps from the caudal region of a medium-sized individual. These vertebral centra, as well as others found in Antarctica, show the characteristic *Lystrosaurus* form and structure, that is relatively short anteroposteriorly in relation to diameters, and very deeply amphicoelous. Indeed, the anterior and posterior surfaces of the centrum almost meet in the center of the bone, as is shown by a natural longitudinal section of AMNH 9328 in figure 12.

SHOULDER GIRDLE AND FORELIMB

Among the postcranial bones of *Lystrosaurus* collected at McGregor Glacier are a scapula, a crushed humerus, a radius, some foot bones, and a rib in close association and obviously belonging to a single individual. These bones (AMNH 9514), representing a rather large *Lystrosaurus*, are shown in figure 13.

The scapula, whose medial surface is exposed, is a broad bone, expanded along its vertebral edge. It may be compared with the scapula of *Lystrosaurus* figured by Broom (1903, fig. 1) and a scapula from a partial skeleton of *Lystrosaurus murrayi* (AMNH 8250) from South Africa. The Antarctic



FIG. 13. *Lystrosaurus* sp., AMNH 9514. Slab containing right scapula, distal end of humerus, radius, foot bones, and portion of rib. Approximately $\times \frac{1}{3}$.

specimen is somewhat wider in proportion to its height than either of the South African specimens, and this may be regarded as a function of its larger size. The vertebral edge of the Antarctic specimen is broadly convex, and there is a robust acromion process.

Another partial skeleton from Graphite Peak (AMNH 9559) represents a small individual, whose scapula is less than one-third the height of AMNH 9514 and about half that of the South African specimen AMNH 8250. It is a slender bone, as would be expected in such a small specimen. These scapulae are shown in figure 14, which also includes for comparison the scapula of *Lystrosaurus hedini* from Sinkiang, China, figured by Young (1935, fig. 5).

The partial skeleton (AMNH 9559) includes a very good sternum (fig.

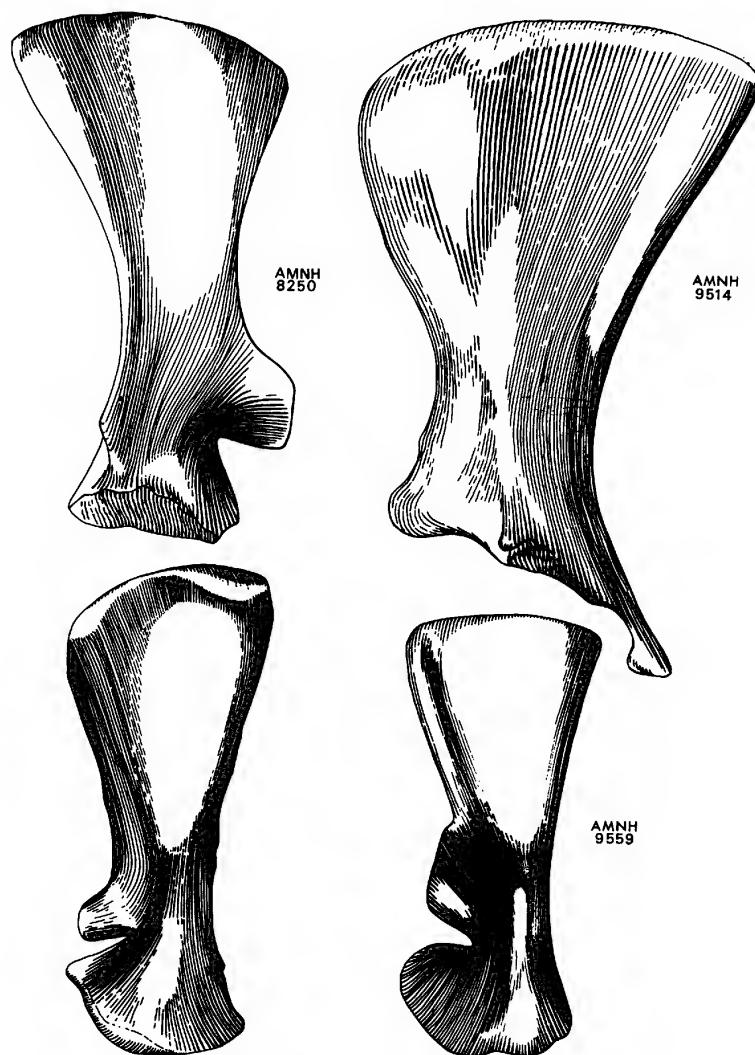


FIG. 14. *Lystrosaurus*, lateral views of scapulae. *Lystrosaurus* sp., AMNH 9514, right scapula, from Antarctica, $\times \frac{1}{2}$, compared with *Lystrosaurus murrayi* AMNH 8250, right scapula, from Africa, $\times \frac{3}{4}$. *Lystrosaurus* sp., AMNH 9559, left scapula from Antarctica, $\times 1$, compared with *Lystrosaurus hedini*, left scapula, from China, $\times \frac{1}{2}$.

15). This element is a flat, roughly circular or polygonal bone, a shape characteristic of the sternum in *Lystrosaurus*. It may be compared with the sternum of a *Lystrosaurus* from South Africa figured by Broom (1903, fig. 2)

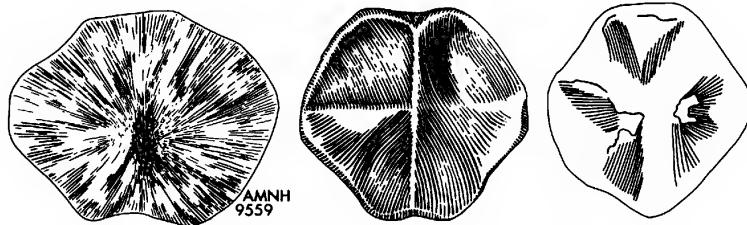


FIG. 15. Three *Lystrosaurus* sterni, in ventral view. *Lystrosaurus* sp., AMNH 9559. $\times \frac{3}{4}$. *Lystrosaurus hedini* Young, from China, after Young, 1935. $\times \frac{1}{3}$, center. *Lystrosaurus* sp., from the *Lystrosaurus* Zone of South Africa, after Broom 1903. $\times \frac{1}{4}$, right.

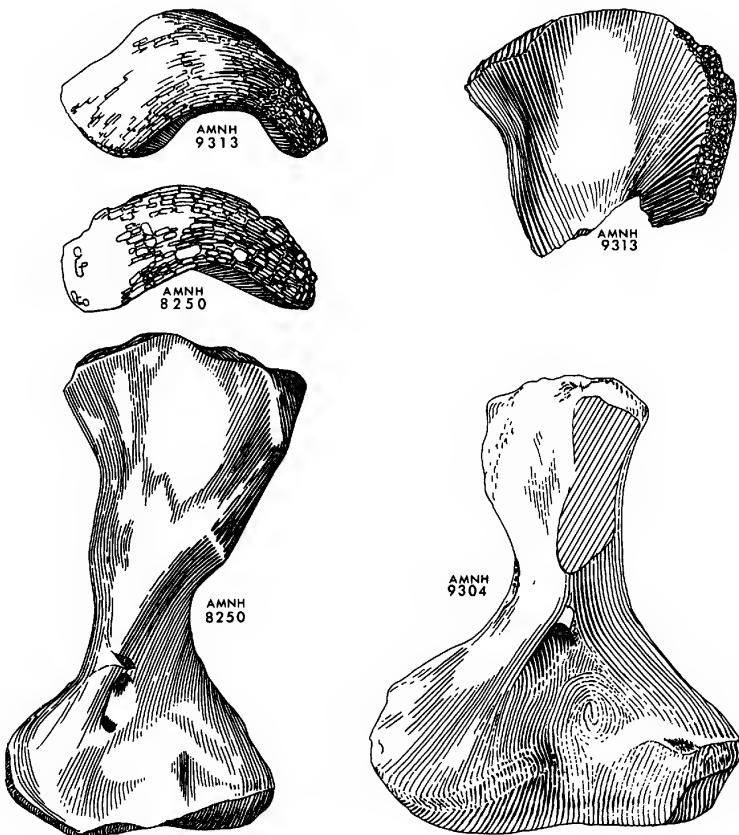


FIG. 16. *Lystrosaurus* sp., AMNH 9304, distal portion of left humerus, anterior view; AMNH 9313, proximal portion of left humerus, anterior and proximal views. *Lystrosaurus murrayi* (Huxley), AMNH 8250, left humerus, from *Lystrosaurus* Zone of South Africa, anterior and proximal views. All $\times \frac{3}{4}$.

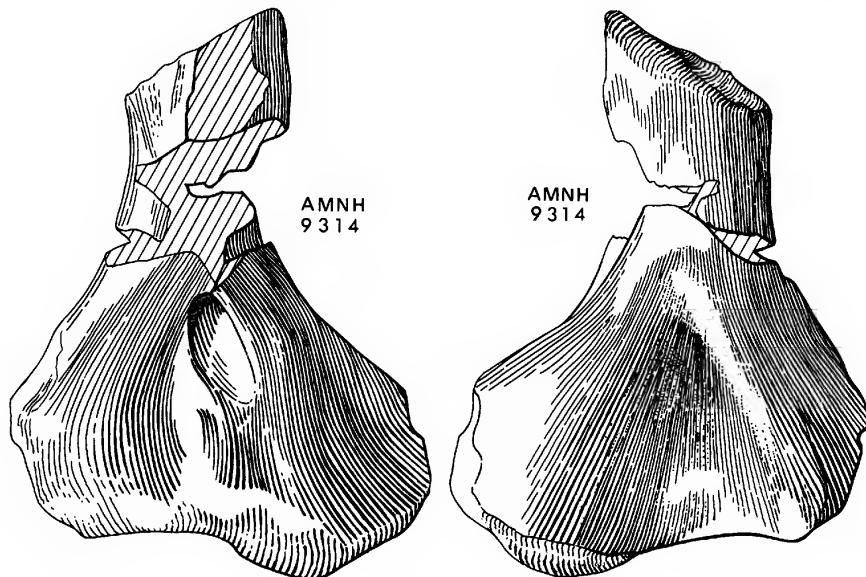


FIG. 17. *Lystrosaurus* sp., AMNH 9314, distal portion of right humerus. Anterior and posterior views. $\times 1$.

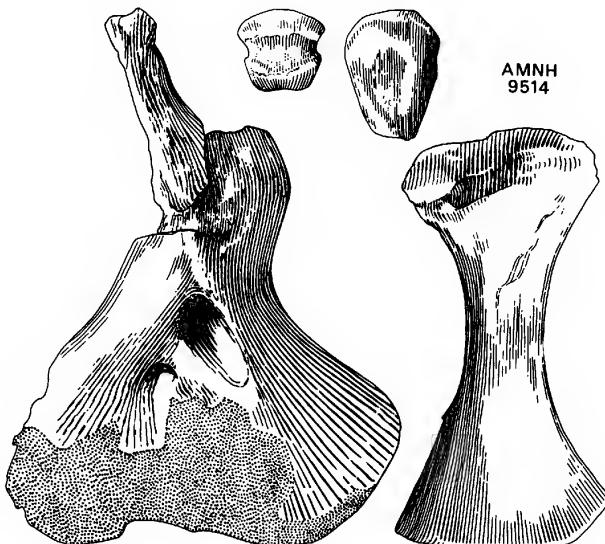


FIG. 18. *Lystrosaurus* sp., AMNH 9514, distal portion of right humerus, radius, and toe bones associated. $\times \frac{1}{2}$. (See fig. 14 for scapula associated with these bones.)

and with that of *Lystrosaurus hedini* from Sinkiang, China, figured by Young (1935, fig. 6).

Humeri are well represented among the Antarctic *Lystrosaurus* materials, especially among the fossils collected at Coalsack Bluff. In the Antarctic specimens the distal end of the humerus is broad, whereas the proximal articulation is strongly bowed. There is a robust deltopectoral crest, and below it a large entepicondylar foramen. These characters, so typical of the humerus in *Lystrosaurus* are shown in figure 16, in which specimens from Coalsack Bluff are compared with the South African specimen (AMNH 8250), and in figure 17, in which the characters of the distal part of an Antarctic humerus (AMNH 9314), particularly the strong development of the entepicondylar foramen, are shown. In the large humerus from McGregor Glacier (AMNH 9514) the distal width is perhaps somewhat exaggerated, owing to crushing of the bone, as may be seen in figure 18.

Figure 18 includes the radius associated with the partial humerus and scapula. It is a relatively short bone, broadly expanded at each end, the distal expansion being especially strong. The proximal articulation is

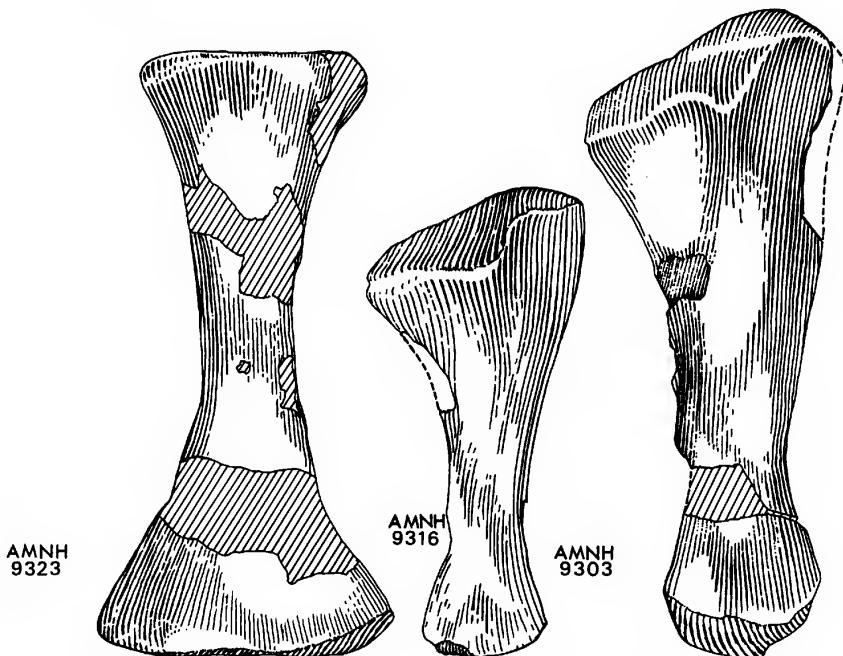


FIG. 19. *Lystrosaurus* sp., AMNH 9323, left radius; AMNH 9316, 9303, left ulnae. All $\times 1$.

rounded. Another, smaller radius (AMNH 9323) from Coalsack Bluff is correspondingly more slender.

Two ulnae from Coalsack Bluff (AMNH 9303, 9316) are of characteristic *Lystrosaurus* form. The proximal end of the ulna is expanded, and its articular face is elongated. There is no olecranon, as Watson (1913) has observed, but the farthest extension of the proximal end of the bone on its external side may indicate an attachment for a cartilaginous process. The two bones are illustrated in figure 19.

The several foot bones, which are a part of AMNH 9514, are of typical *Lystrosaurus* form, indicating a broad, short manus. This is exemplified by the phalanges, which are essentially as broad as they are long. An ungual phalanx is elongated and flat.

PELVIS AND HIND LIMB

A number of bones collected at Coalsack Bluff are from the pelvis. AMNH 9318 is a portion of an ilium; AMNH 9319, a part of an ischium (fig. 20). These two bones, although not found together, are of such size that they may very well be components of a single pelvis. The portion of ilium includes the ventral surface of the anterior notch on the iliac blade, its position being indicated on the reconstruction of the pelvis (fig. 21). *Lystrosaurus* is characterized by two, and sometimes three, large notches incised deeply into the iliac blade, and the presence of such a notch in the Antarctic specimen is conclusive proof that the bone belongs to *Lystrosaurus*. The ischium is a flat bone, and in AMNH 9319 most of the acetabular surface is preserved.

There is a small left pubis (AMNH 9349) from Coalsack Bluff (fig. 20). It shows the deep notch which together with a corresponding notch in the ilium forms the puboischiadic fenestra so characteristic of many therapsid reptiles. This bone also shows an articular surface for its union with the ischium.

Two femora (AMNH 9321, 9322) from Coalsack Bluff, are shown in figure 22. These bones closely resemble the femur as it is known in *Lystrosaurus*. The ends of the bone are expanded, as shown particularly well in AMNH 9321. The articulation with the acetabulum is broad, but there is no well-defined head. There is a well-developed major trochanter.

A block from Kitching Ridge, flanking Shackleton Glacier, contains a part of a foot, probably a pes (AMNH 9565). Three digits are displayed, the first with two phalanges and the next two, each with three phalanges. *Lystrosaurus* is characterized by a reduction of the phalangeal formula in both fore and hind feet to 2-3-3-3-3. The digits are short, and indicate a broad foot typical of *Lystrosaurus*. This specimen is illustrated in figure 23.

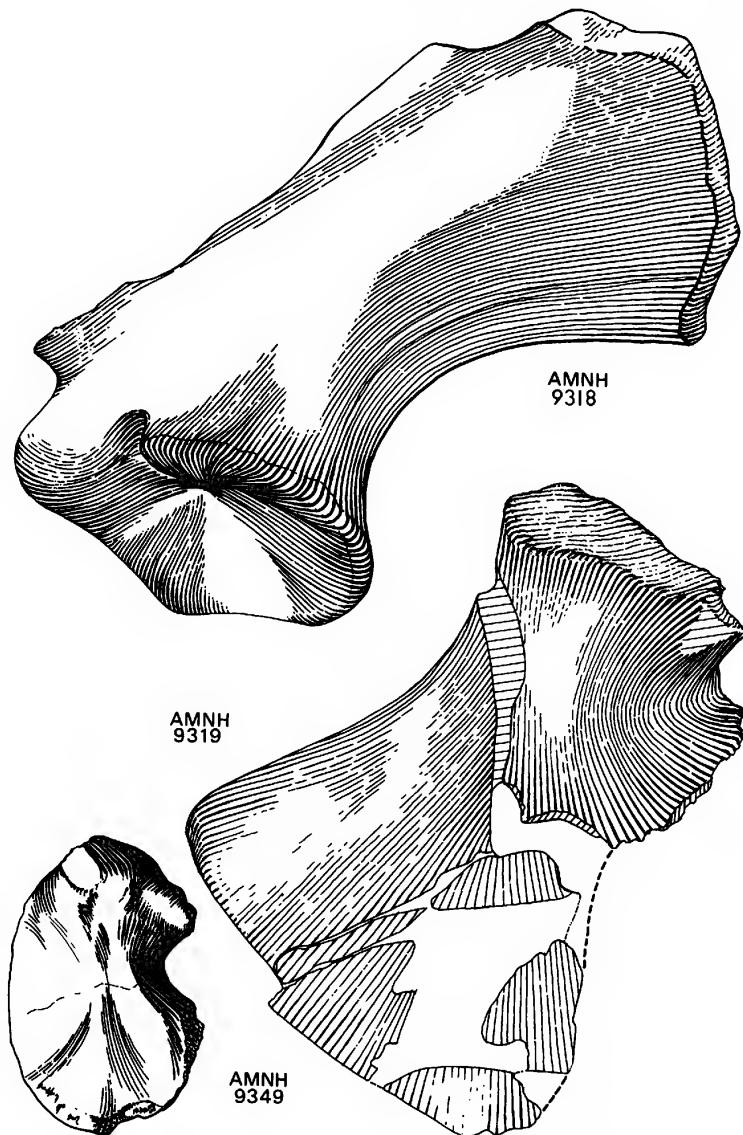


FIG. 20. *Lystrosaurus* sp., AMNH 9318, partial right ilium; AMNH 9319, portion of right ischium, $\times \frac{3}{4}$; AMNH 9349, left pubis, $\times 1\frac{1}{3}$. External lateral views.

DIMENSIONS OF ANTARCTIC FOSSILS

No attempt is made herein to present tables of measurements of the Antarctic specimens of *Lystrosaurus*. In view of the nature of the materials

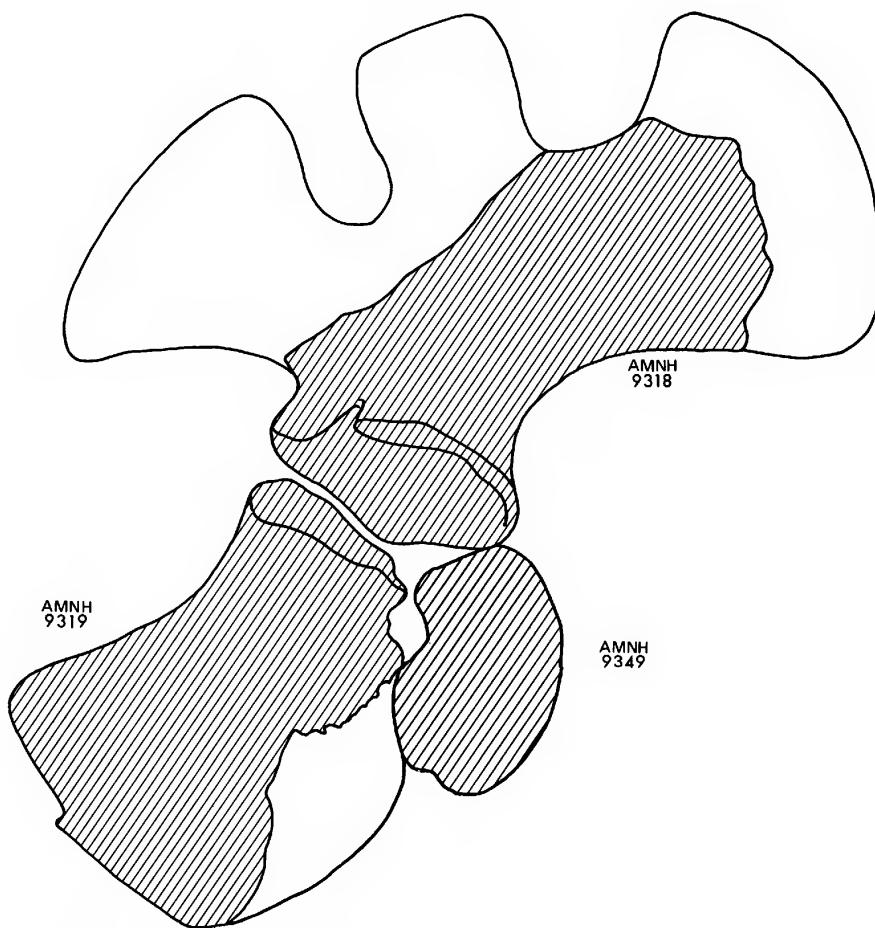


FIG. 21. Restoration of pelvis of *Lystrosaurus*, showing positions of elements illustrated in figure 20.

available, it is believed that any tables of measurements that might be assembled would not be particularly significant. The illustrations are drawn to scale, and show the dimensions and proportions of various portions of skulls, tusks, and selected postcranial elements. Some comparative figures are presented, also. Perhaps these will give a fair idea of the size range in the fossils from Antarctica and their resemblances to certain specimens from Africa and Asia.

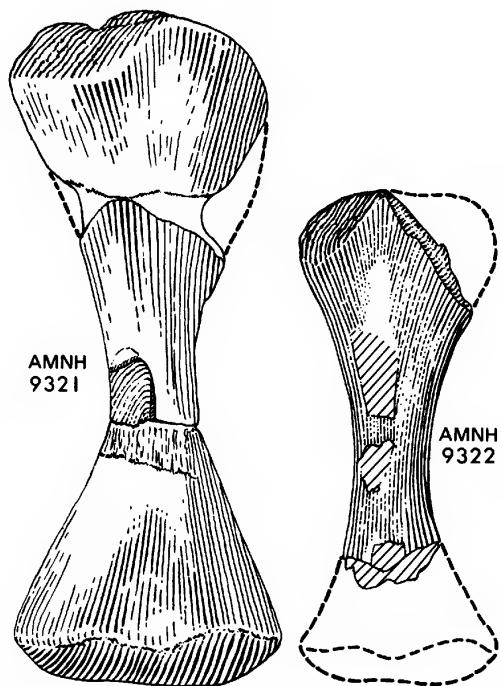


FIG. 22. *Lystrosaurus* sp., AMNH 9321, 9322, left femora. $\times 1$.

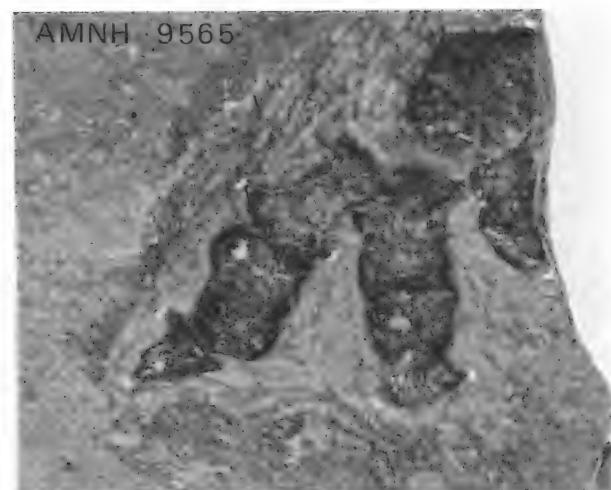


FIG. 23. *Lystrosaurus* sp., AMNH 9565, partial foot. $\times 1$.

SPECIES OF *LYSTROSAURUS*

The identification of two characteristic South African species of *Lystrosaurus*, namely *L. murrayi* and *L. curvatus*, from the Lower Triassic Fremouw Formation of Antarctica is here considered as a fully justifiable procedure. One or more new species might have been created for the Antarctic specimens, but the fossils at hand do not show differences sufficiently great to warrant specific separation from the African species with which they have been aligned. The resemblances truly are striking.

Lystrosaurus was a widely distributed and a strongly specialized reptile during early Triassic time adapted to a particular habitat available across broad and probably uniform expanses of continental terrain. Therefore it is reasonable to believe that speciation was not extreme in this reptile, a conclusion certainly borne out by the fossils. Yet a considerable host of *Lystrosaurus* species has been created, especially among the materials described from Africa, a fact that has been faced during the study of *Lystrosaurus* from Antarctica. Consequently the question as to the validity of the African species of *Lystrosaurus* has necessarily been considered, and this in turn has raised the problem of speciation in this reptilian genus. It is a complex problem, and a digression that cannot be explored in detail now, yet it does deserve some attention because of the implications bearing on continental drift resulting from specific identities of *Lystrosaurus* on the several continents where it has been found.

The problem of species among any fossil tetrapods of such ancient lineage is apt to be vexing. Indeed, the delineation of species among Permo-Triassic amphibians and reptiles in general is commonly more subjective than objective, and this has been particularly true in the case of *Lystrosaurus*. During the years, about 26 species of *Lystrosaurus* in Africa have been named plus an additional species in India and four in China. The diagnoses of these 31 species have been based almost exclusively on characters in the skull and jaw. Some attention has been given to the skeleton, but not so much as should have been the case. The emphasis on skulls is understandable; they are numerous and diagnostic. Distinctive characters in the postcranial skeleton are frequently subtle and difficult to delineate, hence the skull has been favored through the years.

Obviously too many species have been named; consequently several revisions of the genus have been attempted. So far as *Lystrosaurus* in Africa is concerned, particular notice should be given to the revision by Brink (1951) and the review of the genus by Kitching (1968) in his consideration of the *Lystrosaurus* Zone and its fauna. Recently there has appeared a careful study of the genus by Cluver (1971) based on cranial morphology, in which he devotes some attention to the problem of the species that have

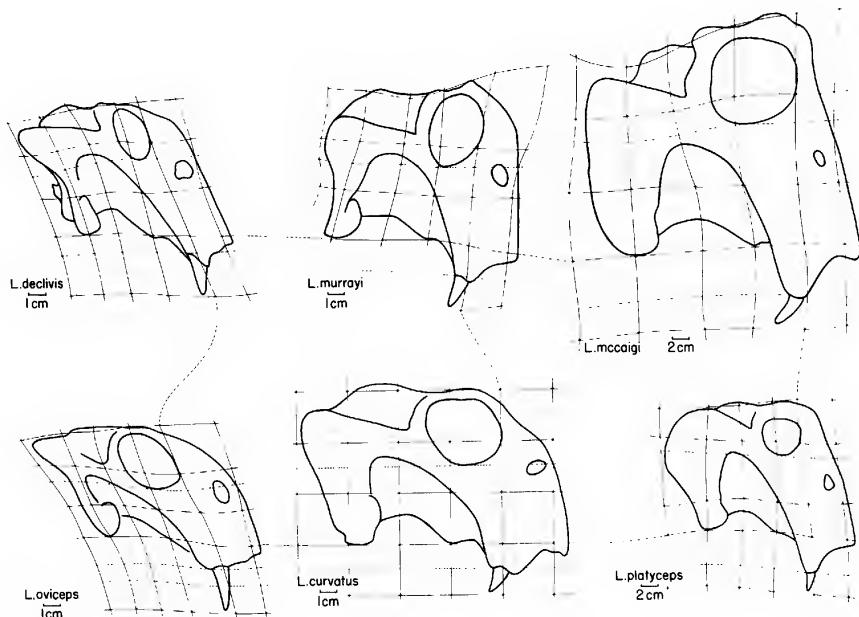


FIG. 24. Comparison of skulls in lateral view of six species of *Lystrosaurus*, by use of Cartesian coordinates. Skull of *L. curvatus* is taken as a central type. In several skulls of species that might have been derived from such a central type, various changes of proportion may be seen. In *L. platiceps* changes involved deepening of skull beneath orbit, with downward elongation of snout. Similar changes are seen in *L. murrayi* and *L. mccaigi*, with, also, an extension forward of skull in front of and above orbit. In *L. declivis*, probably related to *L. murrayi*, deepening of the skull has been accompanied by skewing toward rear. The same is true for *L. oviceps*, but skewing probably occurred independently.

been included in *Lystrosaurus*, not only in Africa, but also in other regions.

The taxonomic proliferation of the African species of *Lystrosaurus* has been variously reduced, to 11 by Brink, to six by Kitching, and to nine by Cluver. If the species on which Cluver and Kitching agree are considered, there are perhaps six valid species, as follows: *Lystrosaurus murrayi* (Huxley), *L. declivis* (Owen), *L. curvatus* (Owen), *L. platiceps* (Seeley), *L. mccaigi* (Seeley), *L. oviceps* (Haughton). These are considered as valid species of *Lystrosaurus* in the present paper.

In India *Lystrosaurus* and associated fossils occur in the Panchet Formation, which is exposed especially well in the Raniganj Coal Field along the Damodar River, northwest of Calcutta. In China there are two areas where *Lystrosaurus* has been found: in the Province of Shansi, in a region

surrounding the city of Wuhsiang; and in Sinkiang, in rocks that have been designated as the Tunghungshan Series.

The occurrences and relationships of *Lystrosaurus* in India have recently been treated in a rather comprehensive paper by Tripathi and Satsangi (1963). These authors recognize *Lystrosaurus murrayi* in the Panchet beds, and of this there can be little doubt; the specimens from India are patently within the limits of *L. murrayi* as it is known in Africa. Tripathi and Satsangi also identify *L. platyceps* among the Indian material and compare some of the fossils from the Panchet beds with the very large African form, *L. mccaigi*. Finally, they have created a new species among the Indian *Lystrosaurus* fossils, namely *Lystrosaurus rajurkari*.

Four species of *Lystrosaurus* have been described from Sinkiang, namely *L. broomi*, *L. hedini*, *L. wiedenreichi*, and *L. youngi*, based for the most part on good materials. *Lystrosaurus hedini*, known from a complete skeleton, is probably a distinct species. The type of *L. wiedenreichi* lacks a skull, so the affinities of this supposed species are difficult to establish. *Lystrosaurus broomi* is close to *L. murrayi* and possibly may be cospecific with the African form, whereas *L. youngi* is close to, if not identical with, *L. curvatus* of Africa. However the supposed species of *Lystrosaurus* in Sinkiang may be viewed, it seems that members of the genus close to, if not identical with, African species extend beyond India into the region now north of the Himalayas.

Lystrosaurus is noted from Shansi but not specifically identified. Dicynodont material from Indo-China, from the vicinity of Luang Prabang, is stated to be "clearly a *Lystrosaurus*, but too poorly preserved for comparisons" (Cluver, 1971, p. 256).

In the light of these considerations, it is here maintained the genus *Lystrosaurus* is composed of eight or perhaps nine species, as set forth below.

LYSTROSAURUS COPE, 1870

Ptychognathus OWEN, 1860 (preoccupied).

Lystrosaurus COPE, 1870.

Ptychosiagum LYDEKKER, 1890.

Mochlorhinus SEELEY, 1898.

Rhabdocephalus SEELEY, 1898.

Prolystrosaurus HAUGHTON, 1917.

TYPE SPECIES: *Lystrosaurus frontosus* Cope = *Dicynodon murrayi* Huxley.

HORIZON AND LOCALITY OF TYPE SPECIES: Lower Triassic, South Africa.

GENERIC DIAGNOSIS: Dicynodont reptiles lacking teeth, but with maxillary tusks present in both sexes. Orbita high, with nares immediately anterior to them. Downward sloping snout, formed by maxilla and premaxilla elongated. Postfrontal present. Eight sacral vertebrae; carpus and tarsus feebly ossified.

Lystrosaurus murrayi (Huxley), 1859

Dicynodon murrayi HUXLEY, 1859.
Ptychognathus verticalis OWEN, 1860.
Lystrosaurus frontosus COPE, 1870.
Ptychognathus boopis OWEN, 1876.
Dicynodon strigops BROOM, 1913.
Lystrosaurus jeppi VAN HOEPEN, 1916.
Prolystrosaurus natalensis HAUGHTON, 1917.
Lystrosaurus broomi YUAN AND YOUNG, 1934. (This species?)
Lystrosaurus rubidgei BROOM, 1940.
Lystrosaurus bothai BROOM, 1941.

TYPE: BMNH¹ R. 1291, an imperfect skull, from the *Lystrosaurus* Zone, Middle Beaufort Beds, Colesburg District, Cape Province, South Africa.

HORIZON AND LOCALITIES: Lower Triassic; Middle Beaufort beds, *Lystrosaurus* Zone, southern Africa; Fremouw Formation, Antarctica; Panchet Formation, India; Tunghungshan Series, Sinkiang, China.

DIAGNOSIS: Skull short and deep, with anterior surface of snout at right angles to skull roof. Frontonasal ridge separating facial from frontal plane, frontal bosses, and median longitudinal ridge on snout present in adults.

Lystrosaurus mccaigi Seeley, 1898

Lystrosaurus putterilli VAN HOEPEN, 1915.
Lystrosaurus amphibius BRINK, 1951.

HORIZON AND LOCALITIES: Lower Triassic; Middle Beaufort beds, *Lystrosaurus* Zone, southern Africa; Panchet Formation, India.

DIAGNOSIS: Very large *Lystrosaurus*, with exceptionally large frontal bosses. Facial plane at right angle to skull roof, snout deep. Nasals in plane of premaxillae, prefrontals protruding forward of midline of facial surface.

There is a possibility that *L. mccaigi* may represent very large individuals of *L. murrayi*, but James Kitching, whose detailed knowledge of Karroo stratigraphy is at present unsurpassed, is of the opinion that the very large *Lystrosaurus* specimens are confined to the lower horizons of the *Lystrosaurus* Zone, whereas *L. murrayi* continues throughout the entire extent of the zone (Kitching, cited by Cluver, 1971). Therefore, as Cluver has suggested, "L. mccaigi is a distinct species which had its main radiation early in *Lystrosaurus* zone times" (Cluver, 1971, p. 250).

Lystrosaurus declivis (Owen), 1860

Lystrosaurus latirostris (OWEN), 1860.
Lystrosaurus alfredi (OWEN), 1862.

¹ British Museum (Natural History), London. Types cited for Antarctic species.

Lystrosaurus depressus (OWEN), 1876.
Lystrosaurus wagneri VAN HOEPEN, 1916.
Lystrosaurus primitivus TOERIEN, 1954.

HORIZON AND LOCALITIES: Lower Triassic; Middle Beaufort beds, *Lystrosaurus* Zone, southern Africa.

DIAGNOSIS: Similar to *L. murrayi*, but with facial plane at obtuse angle to skull roof. Skull very deep, with strong frontonasal ridge and frontal tubercles. Premaxillary facial surface a very flat plane.

Lystrosaurus hedini Young, 1935

HORIZON AND LOCALITY: Lower Triassic; Tunghungshan Series, Sinkiang, China.

DIAGNOSIS: "Differs from all other known lystrosaurids in the remarkable embayment in the lateral palatal rim" (Cluver, 1971, p. 256). Probably allied to *L. murrayi* and *L. declivis*.

Lystrosaurus curvatus (Owen), 1876

Dicynodon curvatus OWEN, 1876.
Lystrosaurus wageri VAN HOEPEN, 1916.
Lystrosaurus jorisseni VAN HOEPEN, 1916.
Lystrosaurus theileri VAN HOEPEN, 1916.
Lystrosaurus youngi SUN, 1964.

TYPE: BMNH R. 3792, a skull, from the *Lystrosaurus* Zone, Middle Beaufort Beds, Elandsberg, Cradock, Cape Province, South Africa.

HORIZON AND LOCALITIES: Lower Triassic; Middle Beaufort beds, *Lystrosaurus* Zone, southern Africa; Fremouw Formation, Antarctica; Lower Triassic, Sinkiang, China.

DIAGNOSIS: A primitive *Lystrosaurus*, morphologically closer to the Permian dicynodonts than any other species of the genus. Snout not produced ventrally so far as in other species of *Lystrosaurus*, and not at such a distinct right angle to skull roof as is frequently the case among other forms. Frontonasal and premaxillary ridges absent, frontal bosses absent. Tusks relatively small. Ventral ramus of squamosal produced posteriorly and flared laterally, in usual *Lystrosaurus* fashion.

Lystrosaurus platyceps Seeley, 1898

Lystrosaurus andersoni BROOM, 1907.

HORIZON AND LOCALITIES: Lower Triassic; Middle Beaufort beds, *Lystrosaurus* Zone, southern Africa; Panchet Formation, India.

DIAGNOSIS: Deep-snouted *Lystrosaurus*, with smooth skull surface. No

angular division between facial plane and skull roof, but transition abrupt, not gradual. Nasals in premaxillary plane.

Lystrosaurus rajurkari Tripathi and Satsangi, 1963

HORIZON AND LOCALITY: Lower Triassic; Panchet Formation, India.

DIAGNOSIS: Skull roof and facial plane meeting in curving surface. Nasal foramen near biting edge of relatively elongated snout. Lacrimals small, encroaching on nasals in form of conical projection.

Lystrosaurus oviceps Haughton, 1915

Lystrosaurus breyeri VAN HOEPEN, 1915.

HORIZON AND LOCALITY: Lower Triassic; Middle Beaufort beds, *Lystrosaurus* Zone, southern Africa.

DIAGNOSIS: Comparatively primitive *Lystrosaurus*, with smoothly curved skull profile, but with frontonasal ridge and frontal bosses. Snout deep.

Lystrosaurus weidenreichi Young, 1939

HORIZON AND LOCALITY: Lower Triassic: Tunghungshan Series, Sinkiang, China.

DIAGNOSIS: This species has been described largely from the postcranial skeleton, thereby making comparisons with other species difficult, if not impossible. Young distinguished this species from *L. hedini* largely upon the basis of the form of the scapula, which has a low acromion, is strongly curved and distally expanded. *Lystrosaurus weidenreichi* may very well be synonymous with *L. hedini*.

As Cluver (1971) has shown, the species of *Lystrosaurus* may be placed within two general categories according to certain morphological features of the skull. In the first group, the skull has a strongly developed snout, the tusks are rather large, there are well-developed excrescences on the skull—frontonasal ridges, frontal tubercles, prefrontal bosses, and longitudinal ridges on snout—and facial plane meets line of skull roof at distinct angle, often a right angle. Within this category may be included *L. murrayi*, *L. mccaigi*, *L. declivis*, and *L. hedini*. The second group is characterized by a moderately developed snout, generally smaller tusks, smooth skull surfaces and the merging of the facial plane into the skull roof along a curve. Within this category may be included *L. curvatus*, *L. platyceps*, and *L. rajurkari*. *Lystrosaurus oviceps* is somewhat intermediate in position, characterized by a skull in which the facial plane and the skull roof are merged along a

curved surface, but in which there are excrescences upon the surface of the skull.

It seems likely that these two groupings represent a dichotomy in the evolutionary development of *Lystrosaurus*. The question of sexual dimorphism immediately comes to mind, however, and must be given serious consideration. Indeed, sexual dimorphism within the dicynodonts in general and within *Lystrosaurus* in particular has received the attention of students since the time of Owen. But Cluver (1971) maintained that careful analyses of specimens of *Lystrosaurus* from stated localities fail to show anything approaching the fifty-fifty ratio that might be expected if sexual dimorphism did indeed exist. Therefore the evidence seems to indicate that the two groups of *Lystrosaurus* species do represent a bifurcation in evolutionary development, with the second of the above delineated groups being the more primitive.

Almost all students of *Lystrosaurus* hold that *L. curvatus*, the central type of the second group described above, is the most primitive species of the genus. It more nearly resembles a Permian dicynodont than any other *Lystrosaurus*, particularly because of its relatively short snout, curved skull profile, and lack of excrescences on the skull. It may be considered a morphologically ancestral lystrosaurid.

From a form such as *L. curvatus*, *Lystrosaurus* evolved on the one hand into *L. platyceps* and *L. rajurkari*, with many of the primitive characters retained, even though skull proportions were modified, and on the other into *L. murrayi*, *L. mccaigi*, *L. hedini*, and *L. declivis* by a strong bending down of the face with relation to the cranium, by a lengthening of the snout, and especially by the development of bony excrescences on the prefrontals, frontals, and nasal bones. *Lystrosaurus oviceps* may be a species well on the way toward specialization along its own line, or it may be an intermediate form.

If *Lystrosaurus curvatus* is accepted as a central type, the morphological adaptations of the skull representing these two broad lines of evolutionary development may be shown by employment of Cartesian coordinates, as seen in figure 24. The deepening of the skull was a universal trend among lystrosaurids beyond the *L. curvatus* stage, it having been effected to a large degree by a downward growth in the region below the lower border of the orbit. In *L. murrayi* and *L. mccaigi*, and perhaps in *L. hedini* to a lesser extent, there was a forward expansion of the skull in front of and above the orbit, thus bringing about the angular relationships between the facial plane and skull roof, so characteristic of these lystrosaurids. *Lystrosaurus declivis* and *L. oviceps* are interesting because in both species the skull is strongly skewed posteriorly. And there is good reason to think that this development

occurred independently in the two species—in *L. oviceps* as a specialization overlying the primitive *L. curvatus* type of skull and in *L. declivis* as a specialization from an *L. murrayi* type of skull.

DISTRIBUTION OF *LYSTROSAURUS*

It may be premature to make generalizations concerning the distribution of the several species of *Lystrosaurus*, but it is interesting that the two central forms, the obviously primitive *L. curvatus* and *L. murrayi*, are the most widely distributed of the species, being found in Africa, Asia, and Antarctica. Perhaps these two species represent an initial radiation of *Lystrosaurus* through Gondwanaland, whereas the other species represent later specializations, locally developed.

Lystrosaurus murrayi in Africa, Antarctica, and peninsular India, *L. curvatus* in Africa and Antarctica, and *L. mccaigi* and *L. platyceps* in Africa and India, lend strong support to existing physical evidence for the ligation of these land masses as part of a Gondwana continent during early Triassic time. As for *Lystrosaurus* in Indo-China and China, two interpretations are possible. Recent evidence seems to indicate that Indo-China may have been once a part of the Gondwanaland continent, situated between the Indian peninsula and Australia. Such a position would explain the presence of *Lystrosaurus* in present-day southeastern Asia. The presence of *Lystrosaurus* in Shansi, and especially in Sinkiang, can also be explained on the basis of an original Gondwanaland distribution, if one is willing to accept the inclusion of much of China within Gondwanaland, as recently has been tentatively suggested by Hurley (1971). Alternatively one must suppose that *Lystrosaurus* arrived in the northeastern part of Asia by a long intercontinental migration from its original homeland—northward through the African portion of Gondwanaland, into Laurasia at the Spanish “hinge” (the Spanish-Moroccan region that served as a connection between the two great supercontinents), and from there to the east into what is now northwestern and central China.

Either interpretation is valid. But the presence of *L. murrayi* and *L. curvatus* in China lends weight to the suggestion that eastern Asia was once a part of Gondwanaland, and that these two species had a continuous range across what are now the distantly separated continents of Asia, Africa, and Antarctica.

CONCLUSIONS

As has been shown in this paper, as well as in previous contributions by the present author and various associates, the presence of *Lystrosaurus* in the Lower Triassic Fremouw Formation of Antarctica can be accepted

beyond doubt. Furthermore, the present paper attempts to show that at least two valid species of *Lystrosaurus* represented in the *Lystrosaurus* Zone in South Africa, namely *L. murrayi* and *L. curvatus*, are present in the Fremouw Formation. *Lystrosaurus murrayi* is found in the Panchet Formation of India, and probably in the Lower Triassic sediments of China as well. It seems probable that *Lystrosaurus curvatus* also occurs in China.

The presence of African species of *Lystrosaurus* in the Lower Triassic beds of Antarctica and in India constitutes strong evidence indicating the close ligation of these now widely separated continents during early Triassic time. Indeed, the occurrence of *Lystrosaurus murrayi* in these regions may be interpreted as the separated remnants of what was once a continuous range of one species, a range comparable in extent to the ranges of many recent species of land-living vertebrates. The implications of these considerations with regard to Gondwanaland and continental drift are of prime importance, and need not be belabored here.

As for *Lystrosaurus* in China perhaps represented by two of the African species, *Lystrosaurus murrayi* and *Lystrosaurus curvatus*, as well as by others peculiar to this part of Asia, two explanations are at present possible. According to one, *Lystrosaurus* may have migrated from Africa into Asia by way of a Moroccan-Spanish connection. According to the other, eastern Asia may very well have been a part of Gondwanaland, as an extension from peninsular India. If this latter interpretation, suggested by Hurley (1971) (among others) is supported by future studies, it will bring all known species of *Lystrosaurus* together within ranges consistent with our knowledge of distributions among various modern land-living tetrapods.

In conclusion, it is justifiable to say that the presence of African species of *Lystrosaurus* in Antarctica is a paleontological fact of extraordinary significance.

ADDENDUM

Since this paper went to press a description by Sun Ai Lin (1973) of two supposed new species of *Lystrosaurus* in Sinkiang has appeared. These are designated as *Lystrosaurus latifrons* and *Lystrosaurus robustus*. The text is in Chinese; unfortunately I have not been able to get an immediate translation, and therefore cannot make a judgment at this time concerning these new Asiatic materials. (See Sun Ai Lin, 1973. Permo-Triassic dicynodonts from Turfan, Sinkiang. Mem. Inst. Vert. Paleont. Paleoanthrop. Acad. Sinica, no. 10, pp. 53-68, pls. 1, 2.)

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